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A winner in the Anthropocene: changing host plant distribution explains geographic range expansion in the gulf fritillary butterfly

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Abstract:

1. The changing climate is altering the geographic distributions of species around the world with consequences for population dynamics, resulting in winners and losers in the Anthropocene.
2. *Agraulis vanillae*, the gulf fritillary butterfly, has expanded its range in the past one hundred years in the western United States. We combined time series analysis with species distribution modeling to investigate factors limiting the distribution of *A. vanillae* and to predict future shifts under warming scenarios.
3. In the western US, where we have time series and geographic data, urban development has a positive association with year of colonization (the host plant *Passiflora* is an ornamental in gardens). Colonization was also associated to a lesser extent with winter maximum temperatures, while a negative impact of minimum temperatures and precipitation was apparent on population growth rates. In the eastern US, urban environments play less of a role and the butterfly is primarily limited by minimum temperatures in the winter and host availability later in the season.
4. Models shows different projections based on region. Eastern U.S. expansion broadly follows the expectation of poleward distributional shifts, especially for the butterfly's maximum distributional extent. Western U.S. expansion is not limited to a single direction and is driven by urban centers becoming more suitable for the host plant.
5. These results demonstrate the value of combining time series with spatial modeling and incorporating biotic interactions to understand and predict shifting geographic ranges in the Anthropocene.

Keywords: *Agraulis vanillae, Passiflora*, climate change, expansion, distribution, model fusion

Introduction

The influences of global change, which include invasive species, overexploitation, and climate change, are impacting species around the world (Butchart et al., 2010). We can expect these factors will have varying effects on different species, and that some species will be "winners" under altered conditions (McKinney & Lockwood, 1999). Identifying successful species and the reason for their success in the face of environmental change is important for understanding the potential of individual species and ecosystems to persist and thrive in future climates. In particular, understanding how aspects of global change negatively impact some species, while benefiting others, will improve our ability to predict future species assemblages. One broad method for assessing “winning” and “losing” is by measuring species distributions, which are already shifting in response to recent change (Chen et al., 2011). For some species, ranges are expanding, while for many others ranges are shifting or contracting (Parmesan, 2006). In the context of warming temperatures, distributional change can by caused by direct effects on development and survival (Crozier, 2004) or by indirect effects mediated by a biotic interactions (Gutierrez & Thomas, 2001). Ectotherms, including butterflies and other insects, are particularly sensitive to changes in the climate and are exemplar species for the study of these issues (Parmesan et al., 1999; Warren et al., 2001). Here we investigate the gulf fritillary butterfly (*Agraulis vanillae)*, which appears to be benefitting from anthropogenic influence and has recently expanded its range in the western United States (Shapiro, 2007). In this study we seek to better understand the drivers underlying this expansion using a combination of spatial occurrence data and long-term population records.

Agraulis vanillae is a neotropical butterfly associated with riparian and weedy or disturbed habitats (Shapiro, 2009). Over its entire distribution, from temperate North America to temperate South America, there are eight identified sub-species. Previous work has demonstrated genetic divergence between North American and South American lineages (Runquist et al., 2012). In the United States, *A. vanillae* is multi-voltine and in warmer southern regions flies almost all year (Sourakov, 2008). Eastern populations are known to undergo poleward movement each year (Walker, 1991), with sightings as far north as North Dakota and New York (Scott, 1986). The butterfly has a known sensitivity to frost, which can be lethal to all life stages (Shapiro, 2007) and may limit its permanent overwintering distribution. This raises the possibility that the recent expansion of this butterfly is from the direct effect of rising temperature reducing the risk of extinction along the northern range margins in the winter.

Agraulis vanillae utilizes most plants from the genus *Passiflora* as hosts (May, 1992). The two most common species in the United States are *Passiflora incarnata* and *Passiflora lutea*, both of which grow naturally across much of the southeastern United States (Gremillion, 1989). *Passiflora* prefers well-drained soils and is often found in disturbed sites. In the western United States, *Passiflora* is not present in natural areas and is restricted to modified landscapes and gardens, as various species have been introduced to urban areas as ornamentals (Graves & Shapiro, 2003). We are not aware of any instances where the plant has escaped urban confines and established large self-sustaining populations. Winter freezing temperatures likely limit the distribution of the plant in the wild, however survival can be improved by active management in cultivated populations (McGuire, 1999). *A. vanillae*

was first reported in Southern California in 1875 and in San Francisco as early as 1908. It did not permanently establish in San Francisco until 1955, where it used *Passiflora* (Powell, 2000). In the 1960's and 1970's the butterfly briefly established in Sacramento but was extirpated and has only recently reestablished in the region. The human-propagated expansion of *Passiflora* in urban centers offers an alternative biotic explanation for the expansion of the gulf fritillary.

In this study, we utilize time series analysis and species distribution modeling to address the following questions. First, using data from a long-term observational study, we ask if climate or urban development better explain the establishment and success of the butterfly in recent years in the Sacramento Valley. Second, using citizen science occurrence data and species distribution modeling, we ask if the current distribution of the butterfly in the continental United States is better explained by host plant or climate limitation and how this varies by region. Finally, we ask if the butterfly is likely to continue to expand its distribution under different climate change scenarios.

Materials and methods

Sacramento Valley time series data

Long-term observational data were collected every other week by a single observer (AMS) across five sites in the Sacramento Valley. Count data of individual butterflies at these five sites have been collected since 1999 and presence/absence data have been collected since the 1970's or 1980's, depending on the site. Site descriptions and additional details have been reported elsewhere (Forister et al., 2010). *Agraulis vanillae* did not

consistently appear at any of these five sites until 2001 and did not appear at every site until 2012. Climate data in California were derived from 270m grid climate maps of monthly and annual values for minimum and maximum temperature and precipitation (Flint & Flint 2012; Flint et al. 2013; Thorne et al. 2015). We extracted the values for grid cells that overlapped with each of the sample sites in the Sacramento Valley and averaged the values for each monthly variable for each year. We calculated seasonal variables by further averaging monthly values to season and converting to water year (the start of September through the end of August).

Sacramento Valley statistical analysis

We approached the analysis of times series data in two phases. First, we used annual presence/absence data to examine colonization, attempting to model the difference between years in which the butterfly was absent across our focal sites and years in which it was resident (spanning 1984 through 2018). Residency at a site was determined to be a presence in consecutive years. Random forest regression was used with presence at a site (during years of residency) in a given year as the response variable and year, percent urban land cover (at a county level), seasonal means of minimum temperature, seasonal means of maximum temperature, and seasonal means of precipitation as covariates. A total of 500,000 trees were made with a node size of 5. Variable importance was determined by examining the increased mean squared error of the model when each variable was randomly permuted. The most influential variables identified by random forest analysis were moved forward into a Bayesian hierarchical linear regression. While the random forest is useful for judging the potential importance of a large

number of variables, including some that are highly correlated, the Bayesian model allows us to estimate coefficients and associated uncertainty in a hierarchical framework (simultaneously within and across sites). Following a previous model used for data from these study sites (Nice et al, 2019), presence was modeled both at the individual site level and at a higher level across all sites using a Bernoulli distribution. Vaguely informative priors were used for means and variance, with means drawn from normal distribution (mean = 0, sd = 10,000) and variances drawn from a gamma distribution (r = 2, lambda = 0.01). The Bayesian model was comprised of four chains each run for 100,000 iterations with a burn in phase of 50,000 iterations.

As a second phase, we examined annual population dynamics post-colonization at the same focal sites, using individual survey count data summarized by year and transformed into population growth rates. Population growth was calculated as the natural log of the current year's total count divided by the previous year's total count (Sibly & Hone, 2002). To determine the most influential climate variables, population growth in a given year was then modeled using a random forest regression. Covariates in the model included year, urban development, abundance in the previous year, seasonal means of minimum monthly temperature, seasonal means of maximum monthly temperature, seasonal means of precipitation, and these same variables lagged by one year to allow in particular for effects mediated through host plants. Again, a total of 500,000 trees with a node size of 5 was used. Variable importance was determined by examining the increased mean squared error of the model following permutation of each variable, and this was done both within and among sites. Like the colonization analysis, the most influential variables identified by random forest analysis were moved

forward into a Bayesian hierarchical model in which population growth was modeled both at the individual site level and at a higher level across all sites using a normal distribution. Means of covariates were drawn from an vaguely-informative normal distribution (mean = 0, sd = 10,000) and variances were drawn from a gamma distribution (r = 2, lambda = 0.01). This model was comprised of four chains each run for 100,000 iterations with an burn in phase of 50,000 iterations. All analyses were conducted using the randomForest (Liaw & Wiener, 2018) and jagsUI (Kellner, 2019) packages in R Studio.

National data

For US-wide spatial analyses, geo-referenced data points for both *A. vanillae* and *Passiflora* were acquired from observations on iNaturalist and GBIF. Additional observations of *Passiflora* were obtained from Calflora and additional observations of *A. vanillae* from the Butterflies and Moths of North America and eButterfly. Only observations since 2000 with a spatial precision higher than 1km were used for analysis. Both *Passiflora* and *A. vanillae* are distinct and identification is likely not a concern, however a random subset of 100 observations with photos were checked and all were found to be correct IDs. Current climate data and future projections were obtained from WorldClim (Hijmans et al., 2005). A human population density raster was obtained from the Socioeconomic Data and Applications Center, which used data from the 2010 census (Center for International Earth Science Information Network, 2018). All raster layers were cropped to include only the 48 contiguous states of the USA, although *A. vanillae* is also present in Hawaii as an introduced species. Finally, *A. vanillae* points were separated

based on being from the overwintering season, which was defined as between January and March, which is earlier than the earliest observed spring migrant from a study of *A. vanillae* seasonal movement in Florida (Walker, 1991).

National statistical analysis

Species distribution models were built for both *Passiflora* and *Agraulis vanillae.* All host plant models were built at the genus level, but *Passiflora* species known not to be hosts were excluded. The western and eastern distributions were modeled separately, to allow for the possibility of different factors affecting range limits in the different regions. For all models, we used the MaxEnt algorithm, which models presence only data by comparing observations with random background points. For every model, 10,000 random background points were taken within the continental United States. To account for sampling bias in the occurrence data, the random background points were spatially structured using a bias file (Phillips et al., 2009). For *Passiflora,* the bias file was built from all Malpighiales observations (excluding *Passiflora)* and the bias file for *A. vanillae* was built using all Nymphalidae observations (excluding *A. vanillae*). *Passiflora* was modeled using temperature, mean precipitation, and human population density as covariates. Models were built and evaluated using minimum temperature in the coldest month, mean annual temperature, maximum temperature in the warmest month, and both maximum and minimum together as temperature variables. Human population was included in the model to account for any dependence on urban cultivation, which we hypothesized is important in the western United States. The best performing host plant model was later used

as a covariate for the butterfly distribution model. For *A. vanillae,* both the overwintering and maximum distributions were modeled. The overwintering distribution was modeled using the best performing *Passiflora* distribution model and temperature variables. The maximum annual distribution was similarly modeled using the *Passiflora* distribution model and temperature as covariates. As with *Passiflora* analyses, various temperature variables were used for model building and comparison, and only the highest performing model for both overwinter and dispersal distributions were used for inference and projection. The models were trained on 70% of the data and tested with the remaining 30%. Model evaluation was performed by examining the AUC scores and omission error rates of both the real model and 1000 permuted null models. Methods and code for null model permutation are described by Bohl et al. (2019), but briefly, observations from the real model are randomly moved around the study area and compared to the real model using the same covariates and testing data. All analyses were performed in R Studio using the dismo package (Hijmans et al., 2013).

Results

Time Series

For the first twenty-five years of the time series, *Agraulis vanillae* only appeared as an occasional visitor, however beginning in 2001 it became a frequent visitor to all sites across the Sacramento Valley. This rise in the presence of *A. vanillae* occurred during a time of rising temperature and increasing urban development in the area (fig. 1). The random forest model attributed high importance to winter maximum temperatures, percent urban land cover, and year in predicting presence at a site (fig. 2a). Both maximum

temperature and urban land cover were increasing over time, especially land cover, which is highly correlated with year (correlation coefficients for year and land cover range from 0.973 in Solano county to 0.989 in Yolo county). In the Bayesian analysis, the model successfully converged (as judged by visual inspection of posterior probability distributions, Rhat values, and effective sample size estimates) at both the individual site level and at the higher across site level. Only year was used in the model as it is highly correlated with urbanization (precluding the inclusion of both variables). The Bayesian model confirms that both maximum winter temperatures and year are positively associated with colonization at the higher across site level (fig. 3a). Specifically, the probability that maximum temperature has a greater than zero effect is 0.98 and the probability that year has a greater than zero effect is 0.92. There is a 0.98 probability that year has a stronger effect than winter, thus the positive trend of colonization is not sufficiently explained by climate.

For annual population dynamics (represented by the natural log of the current to previous population density), the random forest analysis attributed high importance to abundance in the previous year, winter minimum temperature in the current year, winter precipitation in the current year, and summer precipitation in the current year for predicting population growth (fig. 2b, fig. S1). Urbanization, while one of the covariates in the model, was not found to be important for population growth rates. Coefficients in the Bayesian model for population growth converged at both the across site and individual site level. Previous year's abundance, winter minimum temperature, and winter precipitation all had negative effects on population growth. The model is confident in the negative impacts of previous year's

abundance, winter minimum temperature, and winter precipitation (fig. 3b). Specifically, the probability that previous year's abundance has a negative effect is 0.84, the probability that winter minimum temperature has a negative effect is 0.80, and the probability that winter precipitation has an effect is 0.88. There does not appear to be a strong effect of summer precipitation in the Bayesian hierarchical regression, despite the importance attributed to it in the random forest. All three variables have approximately equal estimated effect sizes. At the individual site level, there is variation in estimated effects, however negative density dependence is observed at all sites. Winter climate is also important at all sites, however some sites have higher estimated impacts of winter precipitation while others more heavily weight winter minimum temperatures (fig. S4).

Species Distribution Models

The predictors of highest importance of geographic distribution of *Passiflora* vary between the eastern and western United States. In the East, *Passiflora* is best predicted winter minimum temperatures and precipitation while in the West urban population and maximum summer temperatures are the best predictors (Table S1, Table 1). All models achieved high AUC values and performed exceptionally well when compared to permuted null models (Table 1, fig. S5). Under the RCP 4.5 scenario, suitable habitat in the eastern US is predicted to increase along *Passiflora'*s, northern range boundary. Habitat is also predicted to become slightly less suitable along the southern range boundary, however the magnitude of this change in suitability is not comparable to the increase on the poleward margin (fig. 4; fig. 5). In the

western U.S.A., current areas of suitability are predicted to expand, but not in a clear poleward direction.

The current overwintering ranges of *A. vanillae* in the eastern and western U.S.A. are best explained by both host plant and winter minimum temperatures (Table S1). Like the host plant model, all models performed well in regard to AUC scores and in comparison with permuted null models (Table 1, fig. S5). The variable importance of minimum temperature in the East is slightly greater, however it is not clear if these slight differences in variable importance are meaningful (Table 1). Future climate scenarios project a slight increase in the suitability of some areas in the southeast for overwintering, but not a major expansion (fig.4; fig. 5). The models of maximum annual distribution tell a different story. Models for maximum annual distribution performed best using average temperature, however greater importance in both regions was given to host plant distribution (Table 1). Again, models performed well using both the AUC metric and permuted null model comparison (Table 1, fig. S5). This greater importance of the host plant is reflected in the future model predictions, which shows *A. vanillae* expansion into areas that also predict *Passiflora* expansion (fig. 4, fig. 5). Thus, while overwintering gains appear marginal under future warming, expansion of the range during the spring and summer is potentially substantial. Across all models, projections under RCP 8.5 show a slightly greater expansion but do not dramatically vary from RCP 4.5 predictions (fig. S6).

Discussion

Species are currently encountering novel biotic and abiotic conditions, which can positively or negatively impact population dynamics and geographic distributions (McKinney & Lockwood, 1999). Building models that parse these various stressors furthers our understanding of these impacts and allows for better prediction of future assemblages. In this study, we found that years in which the butterfly had colonized our focal sites were characterized by warmer winter maximum monthly temperatures, while winter minimum temperatures had a negative impact on population growth rates in the years after colonization. In particular, if the previous winter was cooler and drier, the butterfly was found in higher abundance the next year. It is possible that the negative impact of winter climate on *A. vanillae* that we have observed is mediated through interactions with host plants or other insects. It could be the case that warmer and wetter winters negatively impact *Passiflora*, but another and perhaps more likely explanation is that wetter and warmer winters increases parasitoid pressure and/or disease leading to reduced adult emergence the following year (Harvell et al., 2002; Stireman et al., 2005). *A. vanillae* is known to host nucleopolyhedrovirus (Rodriguez et al., 2011), which could be one mechanism that generated the observed negative density dependence (fig. S1), however this is not known to impact California populations. Finally, at our focal sites there is a slight positive trend over time in winter precipitation and winter minimum temperature (fig. S7), suggesting that if anything the butterfly is persisting and expanding in the Sacramento Valley despite climate, not because of it.

The local impact of climate on the population dynamics of *Agraulis vanillae* in the Sacramento Valley also has implications for explaining the limiting factors of its current distribution in the western United States.

Distribution models of *A. vanillae* in the east and west place high importance on the distribution of the host plant, however only the western host plant model identified human population density as an important predictor (after accounting for sampling bias in the data). One explanation for the recent colonization of the area by the butterfly is thus the increasing urbanization of the Sacramento Valley. Over the past twenty years the suburbs of Sacramento have expanded at a steady rate (Forister et al., 2010), which has likely resulted in an increase in *Passiflora* in the region. Random forest analysis ranked urban land cover over any climate variable when predicting colonization and the Bayesian model found a much greater effect of year (which is highly correlated with urbanization). In the eastern United States, the impacts of temperature, specifically minimum temperatures, are apparent in geographic distribution models. In the east, the distribution of *Passiflora* extends further north in the winter compared to *A. vanillae,* while in the west the overwintering distribution closely resembles that of *Passiflora*. Once the weather warms in the east, the butterflies can then expand to cover the distribution of the host plant. Thus, while minimum temperature plays an important role in the overwintering locations of the eastern gulf fritillary, its maximum extent appears to be host plant limited.

Although all analyses involve a single focal species, an interesting result of our work is the discovery that variation in limiting factors between the east and west result in quite different predictions for distributional change under future climates by season and by region. In the eastern U.S., models using the RCP 4.5 and 8.5 climate scenarios broadly follow the expectation of poleward movement, with more suitable habitat along the northern range margin and a slight reduction in habitat suitability in south. In the winter the

butterfly is limited by temperature and predicted expansion during this time will largely be due to increasing temperatures. Later in the season the butterfly is primarily limited by the distribution of the host plant and this expansion would be better explained by an indirect effect of temperature mediated the distribution of the host plant. In the western U.S., expansion is also predicted, but not in a single direction. This region is much more climactically and topographically complex and this this result is perhaps not surprising. A recognizable pattern is the importance of population centers, especially in the expansion of the maximum annual distribution of the butterfly. It is important to note that our future projections were created using climate forecasts, but not human population forecasts. This means that there is an underlying assumption in the projection that population density will remain the same, which almost certainly will not be met. Given the predictive power of population in the U.S. west in our models, we suggest that this that these projections are conservative. Overall, newly suitable areas for the butterfly closely follow the newly suitable areas for the host plant, thus we infer that expansion in the West is more closely tied to the indirect effect of host plant expansion.

These findings add to the literature stressing the utility of accounting for biotic interactions species distribution modeling and forecasting. Biotic interactions are an important factor in shaping the distributions of species but have been incorporated into few studies examining climate change (Araujo & Luoto, 2007; Heikkinen et al., 2007; Preston et al., 2008; Schweiger et al., 2008), at least relative to abiotic-only distribution models. Many of the studies that do incorporate biotic information demonstrate that, whether the biotic element be a host plant or a mutualist, model performance is

improved. Similarly, we show that the host plant has high predictive importance and allows for a better understanding of the current distributional limits of the butterfly. Another important component of these results is the observed within-distribution variation, as we show the importance of host plant varying by season and region. Recognizing and accounting for this variation is critical in order to better predict future responses to change, especially for species with large spatial distributions (Murphy & Lovett-Doust, 2006; O'Neill et al., 2008). By incorporating both a key host plant interaction and allowing it to vary by region, we have a more complete understanding of this observed expansion.

The gulf fritillary is a notable example of a "winner" in the Anthropocene. While insects are declining on a large scale (Hallmann et al., 2017; Lister & Garcia, 2018; Salcido et al., 2019; Sanchez-Bayo & Wyckhuys, 2019; Wepprich et al., 2019), altered conditions create opportunities for some to prevail. The nuances of each success story are different; but it is clear that increasing temperature is playing a vital role in facilitating the distributional expansion of many of these insect winners. Other studies have shown that rising temperature can impact insect distributions by increasing overwintering survival along a northern range margin (Crozier, 2004), by increasing access to food resources (Raffa et al., 2013), or by increasing diet breadth (Pateman et al., 2012). As temperatures continue to warm, insects will continue to be prime candidates for temperature-driven distributional change, for better or for worse. Continuing to observe these phenomena and developing methods by which to understand them is critical. Here the combination of long-term time series data and large-scale citizen science spatial data allowed for a detailed examination of the underlying causes for

such an expansion. As these types of data continue to become more widely accessible, the common themes behind insect distributional change in the Anthropocene will continue to become more apparent.

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Contribution of authors

A.M.S. collected the Sacramento Valley observational data. J.H.T. and D.P.W. provided the climate data. C.A.H. conducted the species distribution analyses. C.A.H. and M.L.F. conducted time series analysis. C.A.H. and M.L.F. wrote the manuscript with input from co-authors.

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Figure 1. (a) Change in detection probability (the ratio of days observed to total visits) over time across all sites. (b) Annual ratio of urban land cover to total land cover at a county level for the three counties containing long-term study sites: North Sacramento and Rancho Cordova are in Sacramento County; Suisun Marsh and Gates Canyon are in Solano County. (c) Mean monthly maximum winter temperature over time.

Figure 2. (a) Variable importance of model covariates in predicting the presence of *A. vanillae* at a site in the Sacramento Valley over time. (b) Variable importance of model covariates in predicting the annual population growth after establishment.

Figure 3. Bayesian posterior distributions for important coefficients (as determined by random forest). Y-axis shows scaled coefficient estimates. (a) Estimates of coefficients for establishment. (b) Estimates of coefficients for population growth.

Figure 4. Current distribution of suitability for (a) *Passiflora* in the West. (b) *Passiflora* in the East. (c) Overwintering *A. vanillae* in the West. (d) Overwintering *A. vanillae* in the East. (e) Seasonal *A. vanillae* in the West. (f) Seasonal *A. vanillae* in the East.

Figure 5. The expanding gulf fritness landscape. Predicted change in suitability in 2050 under RCP 4.5 for (a) *Passiflora* in the West. (b) *Passiflora* in the East. (c) Overwintering *A. vanillae* in the West. (d) Overwintering *A. vanillae* in the East. (e) Seasonal *A. vanillae* in the West. (f) Seasonal *A. vanillae* in the East.

Table 1. Variable importance and model fit of all species distribution models. Rows represent different regional models and columns are the different variables in the model. AUC (area under the curve) is the performance metric of model fit.

Host Plant Distribution Model							
Region	Max. Temp.	Min. Temp.	Population	Precipitation	AUC	OR	*P*-value
East	10.3	62.9	3.1	23.7	0.822	0.076	**<< 0.05**
West	25.2	16.8	42.2	15.8	0.830	0.125	**<< 0.05**

Overwintering Distribution Model					
Region	Min. Temperature	Host Plant	AUC	OR	*P*-value
East	65.7	34.3	0.931	0.095	**<< 0.05**
West	46.9	53.1	0.855	0.140	**<< 0.05**

Maximum Annual Distribution Model					
Region	Av. Temperature	Host Plant	AUC	OR	*P*-value

East	11.3	88.7	0.843	0.102	**<< 0.05**
West	34.0	66.0	0.821	0.073	**<< 0.05**

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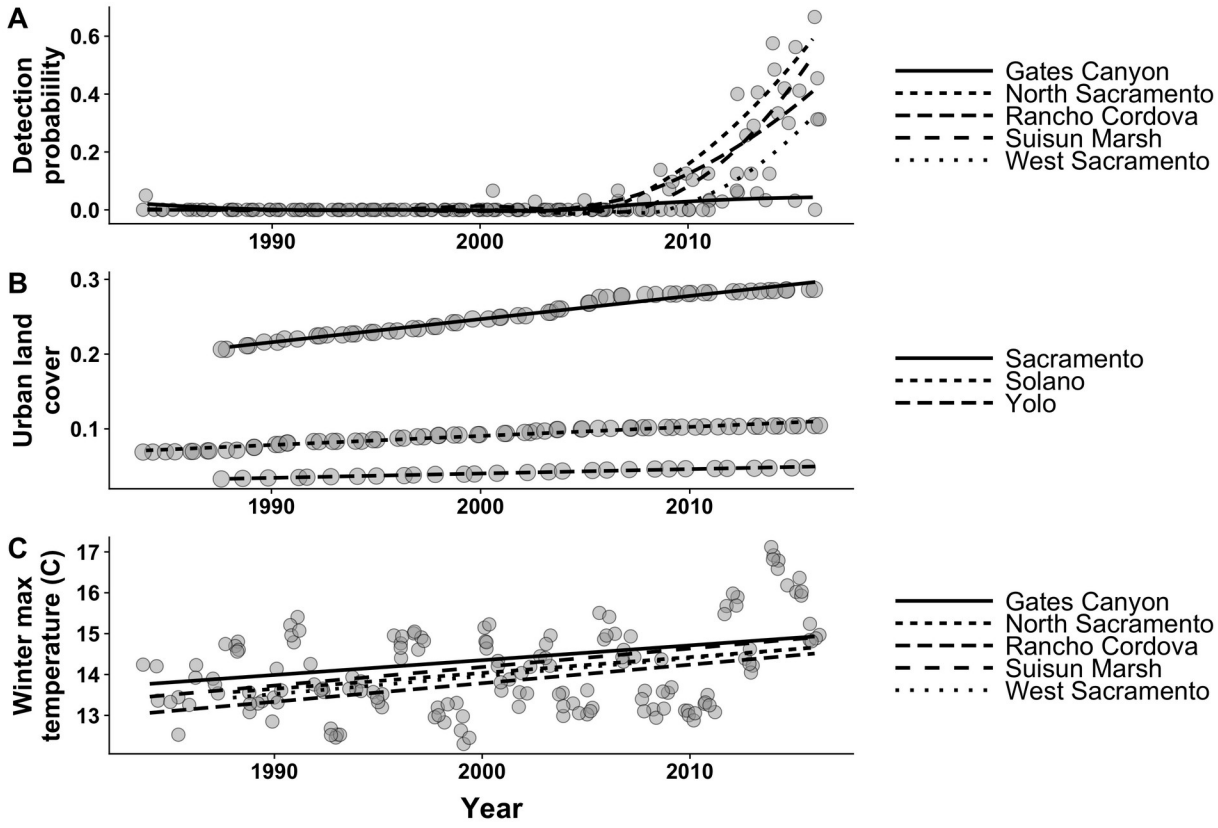
A
Detection probability
0.6
0.4
0.2
0.0
1990
2000
2010
Gates Canyon
North Sacramento
Rancho Cordova
Suisun Marsh
West Sacramento
B
Urban land cover
0.3
0.2
0.1
1990
2000
2010
Sacramento
Solano
Yolo
C
Winter max temperature (C)
17
16
15
14
13
1990
2000
2010
Gates Canyon
North Sacramento
Rancho Cordova
Suisun Marsh
West Sacramento
Year

Figure 1

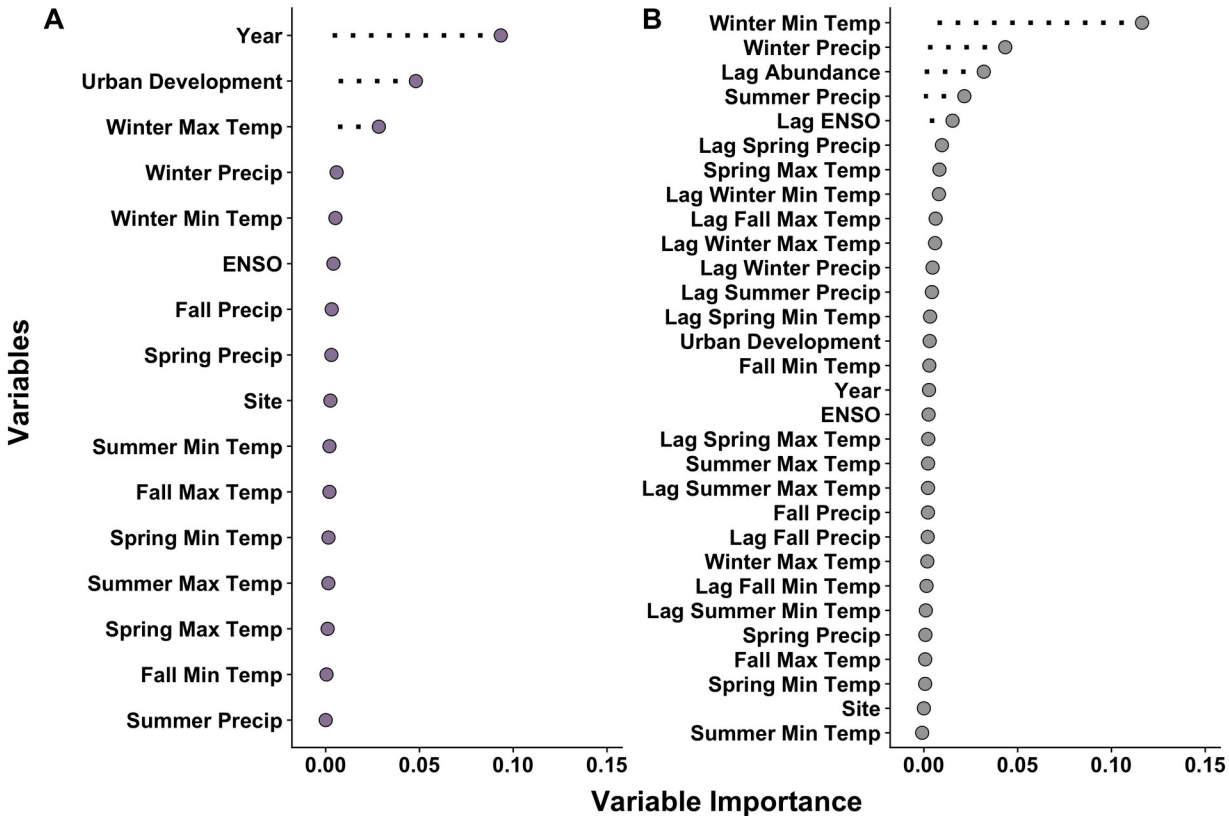
A
Year
Urban Development
Winter Max Temp
Winter Precip
Winter Min Temp
ENSO
Fall Precip
Spring Precip
Site
Summer Min Temp
Fall Max Temp
Spring Min Temp
Summer Max Temp
Spring Max Temp
Fall Min Temp
Summer Precip
Variables
0.00
0.05
0.10
0.15
B
Winter Min Temp
Winter Precip
Lag Abundance
Summer Precip
Lag ENSO
Lag Spring Precip
Spring Max Temp
Lag Winter Min Temp
Lag Fall Max Temp
Lag Winter Max Temp
Lag Winter Precip
Lag Summer Precip
Lag Spring Min Temp
Urban Development
Fall Min Temp
Year
ENSO
Lag Spring Max Temp
Summer Max Temp
Lag Summer Max Temp
Fall Precip
Lag Fall Precip
Winter Max Temp
Lag Fall Min Temp
Lag Summer Min Temp
Spring Precip
Fall Max Temp
Spring Min Temp
Site
Summer Min Temp
0.00
0.05
0.10
0.15
Variable Importance

Figure 2

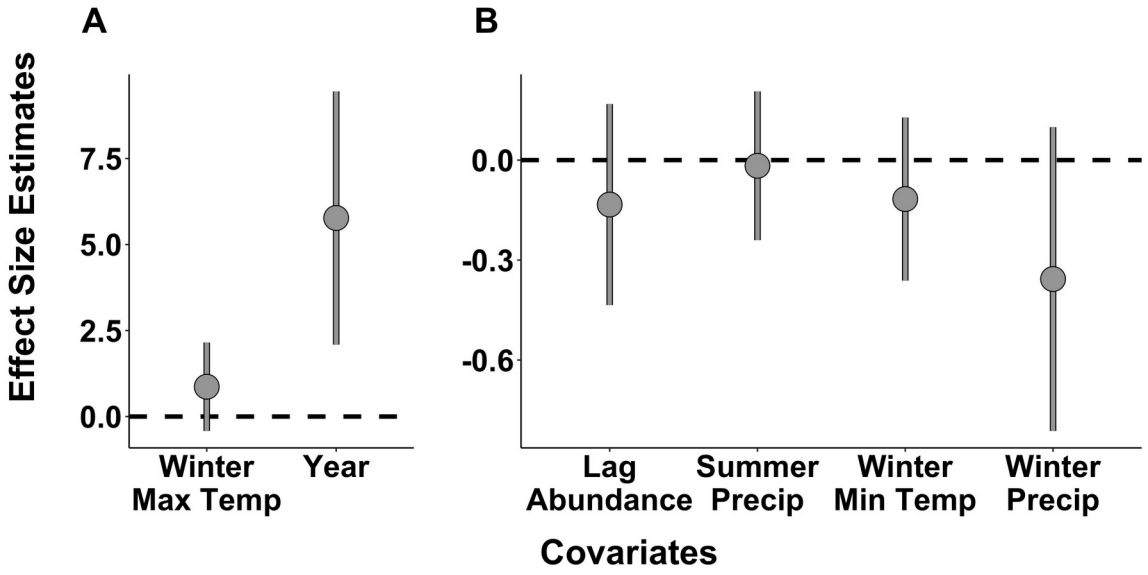
A
B
Effect Size Estimates
7.5
5.0
2.5
0.0
0.0
-0.3
-0.6
Winter Max Temp
Year
Lag Abundance
Summer Precip
Winter Min Temp
Winter Precip
Covariates

Figure 3

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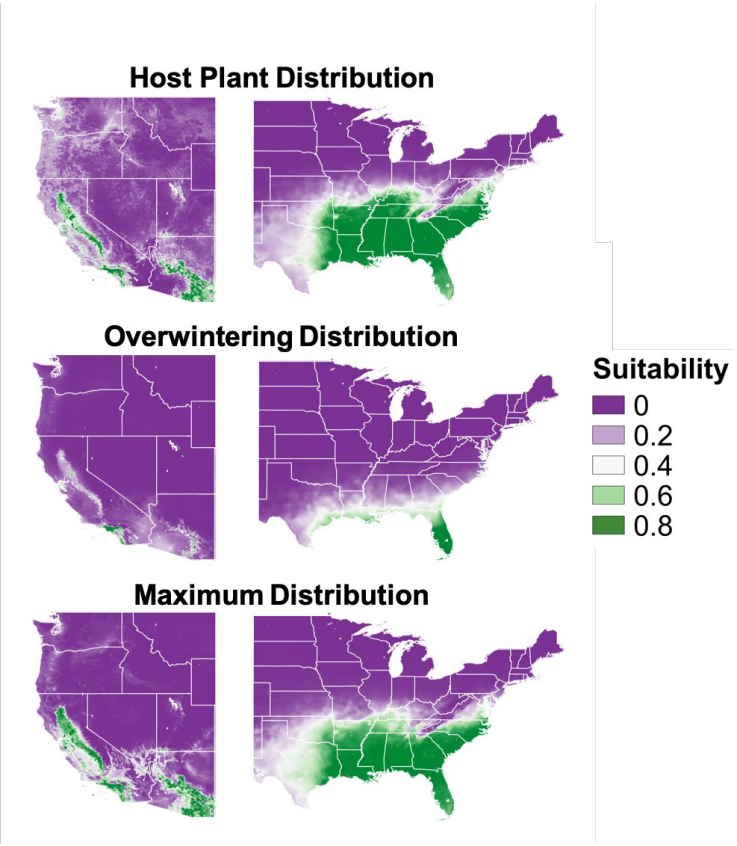

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724 **Figure 4**

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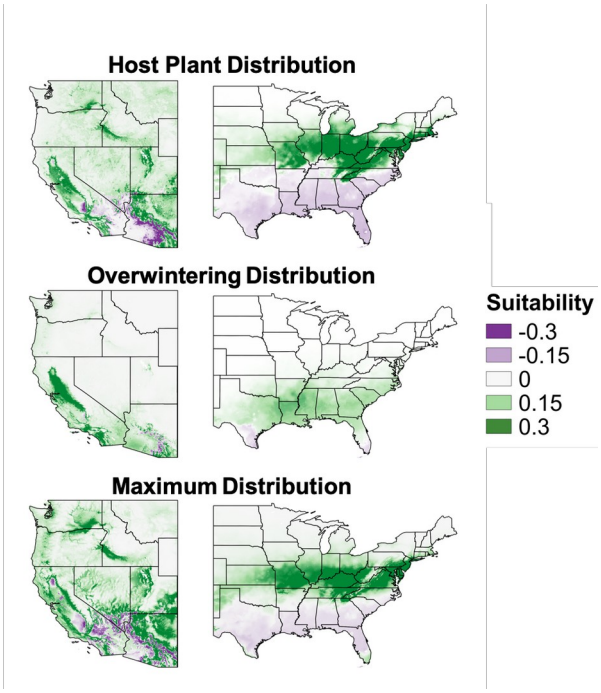
Host Plant Distribution
Overwintering Distribution
Maximum Distribution
Suitability
-0.3
-0.15
0
0.15
0.3

Figure 5